Phytochrome B and at Least One Other Phytochrome Mediate the Accelerated Flowering Response of Arabidopsis thaliana L. to Low Red/Far-Red Ratio

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Phytochrome B and at Least One Other Phytochrome Mediate the Accelerated Flowering Response of *Arabidopsis thaliana* L. to Low Red/Far-Red Ratio[1]

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We have investigated the involvement of phytochrome B in the early-flowering response of *Arabidopsis thaliana* L. seedlings to low red:far-red (R/FR) ratio light conditions. The phytochrome B-deficient *hy3* (*phyB*) mutant is early flowering, and in this regard it resembles the shade-avoidance phenotype of its isogenic wild type. Seedlings carrying the *hy2* mutation, resulting in a deficiency of phytochrome chromophore and hence of active phytochromes, also flower earlier than wild-type plants. Whereas *hy3* or *hy2* seedlings show only a slight acceleration of flowering in response to low R/FR ratio, seedlings that are doubly homozygous for both mutations flower earlier than seedlings carrying either phytochrome-related mutation alone. This additive effect clearly indicates the involvement of one or more phytochrome species in addition to phytochrome B in the flowering response as well as indicating the presence of some functional phytochrome B in *hy2* seedlings. Seedlings that are homozygous for the *hy3* mutation and one of the *fca*, *fwa*, or *co* late-flowering mutations display a pronounced early-flowering response to low R/FR ratio. A similar response to low R/FR ratio is displayed by seedlings doubly homozygous for the *hy2* mutation and any one of the late-flowering mutations. Thus, placing the *hy3* or *hy2* mutations into a late-flowering background has the effect of uncovering a flowering response to low R/FR ratio. Seedlings that are triply homozygous for the *hy3*, *hy2* mutations and a late-flowering mutation flower earlier than the double mutants and do not respond to low R/FR ratio. Thus, the observed flowering responses to low R/FR ratio in phytochrome B-deficient mutants can be attributed to the action of at least one other phytochrome species.

The phytochromes are a family of photoreceptor proteins that control a range of developmental and physiological responses of plants to the changing light environment (reviewed by Smith and Whitelam, 1990). Higher plants possess multiple, discrete phytochromes, the apoprotein moieties of which are encoded by a small family of divergent genes. In *Arabidopsis*, five phytochrome genes, *PHYA* to *PHYE*, have been identified and full-length cDNAs for three of these, *PHYA*, *PHYB*, and *PHYC*, have been cloned and sequenced (Sharrock and Quail, 1989). It has been established by comparing peptide sequences and deduced amino acid sequences that the *PHYA* gene product constitutes the apoprotein moiety of phytochrome A, the well-characterized, light-labile phytochrome species that predominates in etiolated plant tissues (Quail, 1991). The *PHYB* and *PHYC* gene products constitute the apoproteins of phytochromes B and C, which are low abundance, light-stable species of the photoreceptor (Quail, 1991; Somers et al., 1991). The differential patterns of their expression and the diversity among their amino acid sequences are consistent with the suggestion that each of the phytochrome species may play a discrete role in photomorphogenesis (Smith and Whitelam, 1990).

One successful approach to assigning functions to individual phytochromes is the analysis of mutants with deficiencies in individual phytochrome species (Kendrick and Nagatani, 1991; Reed et al., 1992). In *Arabidopsis* two classes of phytochrome-deficient mutants have been identified. The first class comprises the long-hypocotyl, *hy1*, *hy2*, and *hy6* mutants that were selected on the basis of their failure to display normal inhibition of hypocotyl elongation in response to white light (Koornneef et al., 1980; Chory et al., 1989). These mutants, which are severely deficient in spectrally detectable phytochrome, are chromophore depleted and thus are expected to exhibit a depletion in the photochemically active level of both light-labile and light-stable phytochromes (Chory et al., 1989; Parks et al., 1989; Parks and Quail, 1991). Consequently, although of value in the study of phytochrome physiology in *Arabidopsis*, these mutants have been of limited value in assigning roles to discrete phytochrome species. The second class of phytochrome-related mutants carry lesions in the structural genes that encode phytochrome apoproteins.

Recently, the *hy8*, *fre1*, and *fhy2* mutants, which are specifically deficient in *PHYA* transcripts and immunochemically detectable phytochrome A, have been isolated (Nagatani et al., 1993; Parks and Quail, 1993; Whitelam et al., 1993). The *fhy2-1* mutation has been shown to carry a structural alteration of the *PHYA* gene, establishing equivalence of the *PHYA* and *FHY2* loci; thus, the *fhy2* mutant is now referred to as *phyA* (Whitelam et al., 1993). Molecular analyses of mutations

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Abbreviations: FR, far-red light; R, red light; R/FR ratio, the photon fluence rate ratio of red to far-red light in 10-nm bandwidths centered on 660 and 730 nm.

at the *HY8* and *FRE1* loci have shown that these also encode PHYA (P.H. Quail, personal communication; J. Reed, personal communication).

The *Arabidopsis hy3* mutant, which displays a long hypocotyl in white light (Koornneef et al., 1980), has been shown to lack immunochemically detectable phytochrome B (Nagatani et al., 1991; Somers et al., 1991). Recently, the genetic equivalence of the *HY3* and *PHYB* loci has been established (Reed et al., 1993). Compared with wild-type seedlings, etiolated *hy3* seedlings display an extended hypocotyl in R or white light but not in FR light (Koornneef et al., 1980). The *hy3* mutant is also defective in the greening process, producing less Chl and having fewer chloroplasts per mesophyll cell than wild-type plants (Chory, 1992). Light-grown *hy3* plants have very elongated stems, petioles, and leaves and display increased apical dominance (Koornneef et al., 1980; Chory et al., 1989; Reed et al., 1993). The *hy3* mutant is deficient in end-of-day FR light elongation responses and shows an attenuated shade-avoidance response to low R/FR ratio (Nagatani et al., 1991; Whitelam and Smith, 1991; Robson et al., 1993). Similar behavior has been reported for the *lh* (long hypocotyl) cucumber mutant (Whitelam and Smith, 1991; Lopez-Juez et al., 1992) and the *ein* (elongated internode) mutant of *Brassica rapa* (Devlin et al., 1992), both of which lack immunochemically detectable phytochrome B.

The phenotype of light-grown *hy3* mutant plants is similar to the shade-avoidance phenotype displayed by wild-type plants in response to low R/FR ratio conditions. This and the presence of a severely attenuated shade-avoidance response in *hy3* plants have led to the suggestion that phytochrome B plays a significant role in this aspect of photomorphogenesis (Smith and Whitelam, 1990; Whitelam and Smith, 1991). Shade-avoidance responses are not completely absent in the *hy3* mutant, and recently it has been shown to respond normally to low R/FR ratio with respect to leaf area and specific stem weight (Robson et al., 1993).

One of the most obvious responses of *Arabidopsis* plants to low R/FR ratio conditions is a marked acceleration of flowering, displayed in terms of both the time of floral initiation and the number of leaves at flowering (Whitelam and Smith, 1991). It has been noted that the *hy3* mutation causes an early-flowering phenotype (Goto et al., 1991; Whitelam and Smith, 1991). Nevertheless, *hy3* mutants show a slight acceleration of flowering in response to a reduction in R/FR ratio (Whitelam and Smith, 1991; Robson et al., 1993). Since this slight, early-flowering response to low R/FR ratio is observed in a phytochrome B null mutant, the participation of another photoreceptor in the response is implied (Robson et al., 1993). The promotive effect of low R/FR ratio on the flowering of *hy3* plants appears small and is relatively difficult to assess because of the already early-flowering phenotype of the *hy3* mutant.

Several late-flowering mutants of the Landsberg *erecta* ecotype of *Arabidopsis* have been isolated (Koornneef et al., 1991). The *fca, fwa,* and *co* mutants were selected for late flowering under LD conditions. Flowering time in the *fca* mutant is sensitive to vernalization, whereas this sensitivity is reduced in the *fwa* and *co* mutants (Martinez-Zapater and Somerville, 1990; Koornneef et al., 1991; Bagnall, 1992, 1993). Flowering in these mutants is affected by R/FR ratio, being earlier in plants grown under fluorescent plus incandescent light than in plants grown under fluorescent light only (Martinez-Zapater and Somerville, 1990; Bagnall, 1992, 1993). The effect of the lower R/FR ratio is reported to be greatest in the vernalization-sensitive *fca* mutant (Martinez-Zapater and Somerville, 1990; Bagnall, 1992, 1993), and it has been reported that much of the effect of R/FR ratio on flowering time in *fca* disappears following a vernalization treatment (Bagnall, 1993).

In this study, we have investigated the effects of very low R/FR ratio on the flowering of *Arabidopsis* plants that are homozygous for the *hy2* or *hy3* phytochrome-related mutations or the *fca, fwa,* and *co* late-flowering mutations. In addition, R/FR ratio effects have been studied in plants that are homozygous for one or both of the phytochrome-related mutations and one of the late-flowering mutations. All of the late-flowering mutants show a marked acceleration of flowering in response to low R/FR ratio conditions. Also, whereas plants doubly homozygous for *hy3* and a late-flowering mutation also show a marked response to low R/FR ratio, plants that are triply homozygous for *hy2, hy3,* and a late-flowering mutation are early flowering and insensitive to R/FR ratio. These findings implicate phytochrome B and at least one other phytochrome species in the perception of R/FR ratio light signals.

MATERIALS AND METHODS

Plant Material and Growth Conditions

The Landsberg *erecta* ecotype of *Arabidopsis thaliana* L. was the wild type used in this study together with the *hy2-1* (To76) and *hy3-1* (Bo64), phytochrome-related mutants (Koornneef et al., 1980; Reed et al., 1993), and the *fca, fwa,* and *co-3* late-flowering mutants (Koornneef et al., 1991).

Mutants doubly homozygous for *hy2* or *hy3* and a late-flowering mutation were initially isolated as late-flowering, long-hypocotyl plants in F_2 generations derived from crosses of monogenic *hy* mutants with monogenic late-flowering mutants. The phenotype (long hypocotyl but later flowering than monogenic *hy* mutants) was rechecked in the F_3 progeny, and nonsegregating (for both long hypocotyl and late flowering = homozygous) lines were maintained by selfing. Triple mutants were obtained by crossing mutants doubly homozygous for *hy2* and a late-flowering mutation with mutants doubly homozygous for *hy3* and the same late-flowering mutation. Putative triple mutants in the F_2 generation were selected on the basis of an extreme long-hypocotyl phenotype. Nonsegregating lines were crossed to each of the three monogenic mutants to show allelism, thereby also checking the genetic composition of the parental double mutants. The *hy2 hy3* double mutant had a more extreme long-hypocotyl phenotype than monogenic *hy2* or *hy3* mutants and was confirmed to be a double mutant by allelism tests with both parental lines.

Seeds were sown in Petri dishes on 1% (w/v) agar containing BG11 mineral salts (Stanier et al., 1971) and chilled for 4 d at 4°C. Seeds were germinated and grown at 21 to 22°C under continuous white fluorescent light (photon fluence rate, 400–700 nm, = 100 μmol m^{-2} s^{-1}). The seedlings were

selected for uniform appearance, were transplanted into 5-cm pots containing a compost:sand (3:1) mixture, and were grown for a further 7 d under the same light conditions. On d 8 the seedlings were transferred to R/FR ratio growth cabinets.

Light Sources

The R/FR ratio treatment cabinets were the same as those described in detail by Keiller and Smith (1989). The high R/FR ratio cabinet (cool-white fluorescent light) provided a photon fluence rate (400–700 nm) of 100 μmol m^{-2} s^{-1} and an R/FR ratio of 6.81. The low R/FR cabinet (cool-white fluorescent light supplemented with FR) provided the same photon fluence rate (400–700 nm) but an R/FR ratio of 0.13. All light measurements were made using an LI 1800/12 spectroradiometer (Li-Cor, Lincoln, NE).

Measurement of Flowering

Flowering was scored daily, and flowering time is defined as the number of days from sowing for the first petal to become visible in the expanded floral bud. The numbers of rosette leaves were counted at the time of flowering.

RESULTS AND DISCUSSION

The induction of flowering in *Arabidopsis* leads to the transition from vegetative to reproductive development within the apical meristem. Since this transition leads to a cessation of rosette leaf initiation, flowering time and rosette number are correlated. The early-flowering Landsberg *erecta* ecotype of *Arabidopsis*, in keeping with many other LDP's, can be induced to flower early under low R/FR ratio light conditions (Fig. 1, a and e). The flowering response to low R/FR ratio is manifest in terms of flowering time and leaf number, indicating that the early flowering results from a reduction in the period of vegetative development. The phytochrome-related *hy2* and *hy3* mutants flower early, both in terms of flowering time and leaf number, even when grown in a high R/FR ratio (Fig. 1, a and e). Furthermore, growth under low R/FR ratio conditions has only a very small effect on flowering in these two mutants (Fig. 1, a and e). Seedlings that are doubly homozygous for the *hy2* and *hy3* mutations also show little or no response to low R/FR ratio, but it is noteworthy that the double mutant flowers slightly earlier, and with fewer leaves, than either of the monogenic lines (Fig. 1, a and e). This apparent additive effect of the *hy2* and *hy3* mutations implies that seedlings carrying the *hy2* mutation alone must possess some functional phytochrome B. Physiological observations had earlier indicated that *hy2* seedlings retain some active phytochrome (Cone, 1985; Whitelam and Smith, 1991). The earlier flowering of seedlings carrying both the *hy2* and *hy3* mutation, compared with seedlings carrying only the *hy3* mutation, also indicates that in the absence of phytochrome B the reduction in activity of

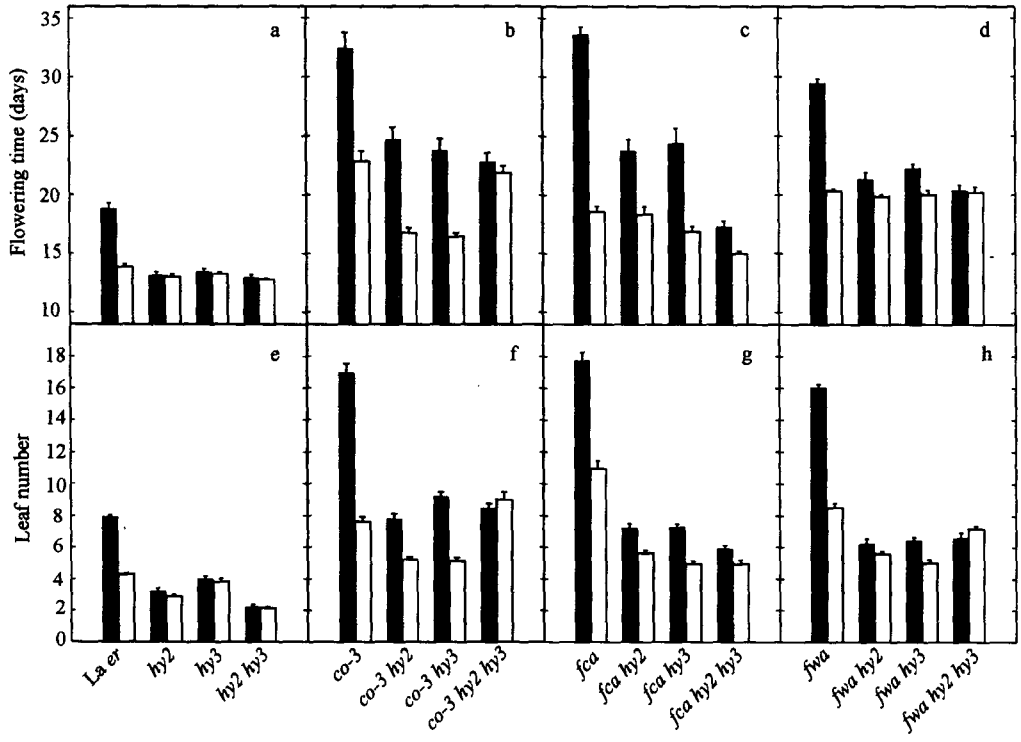

Figure 1. Effect of R/FR ratio on flowering time and leaf number in wild-type, *hy2*, *hy3*, and *hy2 hy3* mutant seedlings (a and e); *co-3 co-3 hy2*, *co-3 hy3*, and *co-3 hy2 hy3* mutant seedlings (b and f); *fca*, *fca hy2*, *fca hy3*, and *fca hy2 hy3* mutant seedlings (c and g); and *fwa*, *fwa hy2*, *fwa hy3*, and *fwa hy2 hy3* mutant seedlings (d and h). Plants were grown under conditions of continuous high (solid bars) or low (open bars) R/FR ratio irradiation. Data represent the means from at least 15 plants, and the error bars are SE.

another phytochrome, as a consequence of the *hy2*-related chromophore deficiency, also leads to early flowering.

The late-flowering monogenic *Arabidopsis* mutants *fca*, *fwa*, and *co-3* have a delayed flowering response in LD growth conditions (Koornneef et al., 1991). This delayed flowering response is also seen when seedlings carrying these mutations are grown in continuous white light (Fig. 1, b–h). All three of the late-flowering mutants show a marked acceleration in flowering when grown in low R/FR ratio conditions, which in terms of both flowering time and leaf number is of more or less the same magnitude as that seen in wild-type seedlings (Fig. 1, b–h). Nevertheless, under low R/FR ratio conditions seedlings carrying the *fca*, *fwa*, or *co-3* mutations still flower later than wild-type seedlings under the same conditions. Thus, the late-flowering phenotype of these mutants is not abolished by growth under low R/FR ratio light. It has been reported that the flowering of the *co-3* mutant is unaffected by R/FR ratio and that only the *fca* mutant shows a significant decrease in flowering time in response to low R/FR ratio (Bagnall, 1993). This conclusion was based on a comparison of flowering times for seedlings grown under fluorescent white light (R/FR ratio approximately 5.0) or under fluorescent white light with supplementary incandescent light (R/FR ratio approximately 1.0). In this study, the low R/FR ratio light source was composed of white fluorescent light with supplementary FR and produced an R/FR ratio of only 0.13. Under these conditions it is was not possible to detect a gradient of responsivity in the various late-flowering mutants. Several other late-flowering mutants of Landsberg *erecta*, including *gi-3*, *fha*, *fe*, *fve*, *fd*, and *ft* (Koornneef et al., 1991) also show an equally pronounced flowering response to low R/FR ratio (G.C. Whitelam, unpublished observations).

The observed responsivity of these late-flowering mutants to extremely low R/FR ratio suggests that this particular phytochrome effect acts to a large extent independently of the factors that control responsiveness to vernalization and daylength, which are differentially affected in the late-flowering mutants. Since mutations in many genes can result in late flowering without abolishing flowering completely, it has been suggested that multiple, parallel pathways control flowering (Koornneef et al., 1991).

Seedlings that are doubly homozygous for *hy2* and one of the late-flowering mutations, or doubly homozygous for *hy3* and one of the late-flowering mutations, flower early in high R/FR ratio conditions (white fluorescent light) compared with seedlings carrying the late-flowering mutation alone (Fig. 1, b–h). In all cases, the flowering of the double mutants is similar to that of the monogenic late-flowering mutants under low R/FR ratio conditions. Growth of these double mutants under low R/FR ratio conditions leads to a significant acceleration in flowering time and reduction in leaf number (Fig. 1, b–h). Thus, it seems that combining the phytochrome-related *hy2* or *hy3* mutations with a late-flowering mutation has, in effect, unveiled a significant shade-avoidance response. One may assume that in the wild-type genetic background flowering is so early in phytochrome B-deficient mutants that a reduction in the level of the active form of other (possibly light-stable) phytochromes by lowering R/FR ratio has little or no physiological effect. The *hy2* mutation would be expected to have a more pronounced effect on the active form of other phytochromes, thereby enabling a slight physiological effect of the *hy2* mutation to be observed in the absence of phytochrome B. In a late-flowering genetic background, flowering is not saturated for earliness by the absence of phytochrome B, thus allowing the effects of low R/FR ratio to be observed.

Seedlings that are triply homozygous for *hy2*, *hy3*, and one of the late-flowering mutations and grown under high R/FR ratio conditions are typically earlier flowering than double mutants carrying only one phytochrome-related mutation (Fig. 1, b–h). Furthermore, when these triple mutants are grown under low R/FR ratio conditions, either a very reduced early-flowering response or no response is observed (Fig. 1, b–h). A small early-flowering response to low R/FR ratio is displayed by *fca* mutants that also carry the *hy2* and *hy3* mutations (Fig. 1, c and g). However, this response is much reduced compared with that displayed by the double mutants. In the case of *fwa* and *co-3* mutants carrying both the *hy2* and *hy3* mutations, a reduction in R/FR ratio appears to cause a slight delay in flowering, measured in terms of leaf number (Fig. 1, b and f, d and h). The loss of the shade-avoidance response in triple mutants that lack phytochrome B and that are phytochrome chromophore-depleted indicates that only the phytochromes are mediators of the flowering response to low R/FR ratio light. Thus, the observed flowering responses to low R/FR ratio in phytochrome B-deficient mutants can be attributed to the action of another phytochrome species and not to the action of some other R- and FR-absorbing photoreceptor.

The observations reported here implicate phytochrome B as a mediator of the early-flowering component of the shade-avoidance syndrome in *Arabidopsis* and also provide strong evidence for the involvement of at least one other phytochrome species in this response. Other authors have reported the failure of phytochrome B-deficient mutants to display elongation growth responses to end-of-day FR light treatments but have noted attenuated elongation growth responses of these mutants to low R/FR ratio conditions (Lopez-Juez et al., 1990; Whitelam and Smith 1991; Devlin et al., 1992). Recently, it has been shown that phytochrome B-deficient *Arabidopsis* seedlings show unmodified retention of some growth responses to low R/FR ratio, namely the reduction in leaf area and specific stem weight (Robson et al., 1993). Thus, although the presence of phytochrome B appears to be correlated with the ability of seedlings to respond to low R/FR ratio by elongation, it is apparently unnecessary for growth responses to low R/FR ratio that involve radial expansion. Shade-avoiding plants that are exposed to vegetational shade channel their resources into elongation growth at the expense of radial or lateral expansion. Thus, the responses to low R/FR ratio that are retained in *hy3* mutants are considered to be related to the shade-avoidance syndrome (Robson et al., 1993).

The phytochrome-mediated acceleration of flowering, partly attributable to phytochrome B but also displayed in the absence of phytochrome B, can also be considered to represent an important component of the shade-avoidance syndrome. Early flowering could be considered to represent the ultimate manifestation of shade avoidance. It is now

evident that this and other aspects of the shade-avoidance syndrome are mediated by multiple phytochrome species, only one of which is phytochrome B.

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